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THE MALE GENITALIA OF BLATTARIA.

1. *BLABERUS* SPP.

(BLABERIDAE: BLABERINAE)

By LOUIS M. ROTH

Pioneering Research Laboratory

U. S. Army Natick Laboratories

Natick, Massachusetts 01760

"Like many other genera the forms of which are variable and the specific features hard to ascertain and express, the genus *Blaberus* has been a despair to the systematist." (Rehn and Hebard, 1927). The use of male genitalia, specifically the aedeagus and preputial spines, has helped to alleviate some of the taxonomic difficulties of several species of *Blaberus*. Burmeister (1838; in Princis, 1946) first mentioned the preputial spines in *Blaberus trapezoideus* Burmeister and Hebard (1917) described them in *Blaberus craniifer* Burmeister and *B. atropos* (Stoll). Princis (1946) illustrated the aedeagus and prepuce of the following species of *Blaberus*: *giganteus* (Linn.), *trapezoideus*, *craniifer*, *atropos*, *discoidalis* Serville, *parabolicus* Walker, *anisitsi* Brancsik, and *boliviensis* Princis. Lefeuvre (1960) illustrated the genitalia of *craniifer*, Quiaoit (1961) described them for *craniifer* and *giganteus*, and McKittrick (1964) illustrated *discoidalis*.

With the exception of Princis (1946) and Lefeuvre (1960), intraspecific variations were not mentioned by the above workers. I have found considerable more variation in *Blaberus* genitalia than was indicated by Princis and Lefeuvre. In this paper I shall illustrate the male genitalia of 12 species of *Blaberus*, describe group and specific differences, including intraspecific variations, and discuss the probable evolution of the aedeagus and prepuce in this genus.

MATERIALS AND METHODS

The following 5 species of *Blaberus* were available in cultures:

craniifer, *giganteus*, *parabolicus*, *atropos*, and *discoidalis*. In addition I have examined the genitalia of museum specimens of these species as well as those of *B. colosseus* (Illiger), *B. brasiliensis* Saussure, *B. minor* Saussure, *B. fusiformis* Walker, *B. scutatus* Saussure and Zehntner, *B. anisitsi* Brancsik, and *B. boliviensis* Princis. Of the 14 *Blaberus* listed by Princis (1963), *assellus* (Thunb.) and *latissimus* (Herbst) were described from nymphs and are questionable species. For reasons given below, I consider *Blaberus colosseus*, which Hebard (1921) synonymized with *B. giganteus*, a valid species and *B. trapezoideus* a synonym of *B. craniifer*.

As suggested by Princis (1946) the tips of the abdomens of dried specimens were dipped in hot water for about a minute, or the specimens were placed in a relaxing chamber. Once softened, the abdomen was slit along the lateral membranes and the genitalia were removed usually without serious damage to the subgenital or supra-anal plates. All specimens were treated with 10% KOH, cleared, and mounted in Permount. The hooked right phallomeres were mounted ventral side up and phallomeres L1 and L2d were mounted dorsal side uppermost. The preparations of the prepuce were spread and flattened to show the spines. This should be taken into account when examining the illustrations. Normally the prepuce partly envelops L2d (see Fig. 121 in McKittrick's 1964 monograph which illustrates the folding of the prepuce in *B. discoidalis*).

Although the principal genitalic characters used are L2d and the prepuce, I have also included photographs of R2 and L1 for comparative purposes. Although these 2 phallomeres are very similar or have minor differences in all species of *Blaberus* (Figs. 1-24) they show family or subfamily differences and their inclusion should be useful in future studies of the genitalia of Blaberidae.

Wherever known I have given locality data for the illustrated specimens, and the identity of the entomologist who determined the species. The abbreviations for the sources of this material are as follows (original geographical source, if known, follows the abbreviations in the explanation of figures): (N) = Natick culture; (ANSP) = Academy Natural Sciences, Philadelphia; (MCZ) = Museum of Comparative Zoology, Harvard University; (L) = Zoological Institute, Lund, Sweden; (AMNH) = American Museum of Natural History; (USNM) = United States National Museum; (BMNH) = British Museum (Natural History). Slides of genitalia are deposited with their respective males in the above museums.

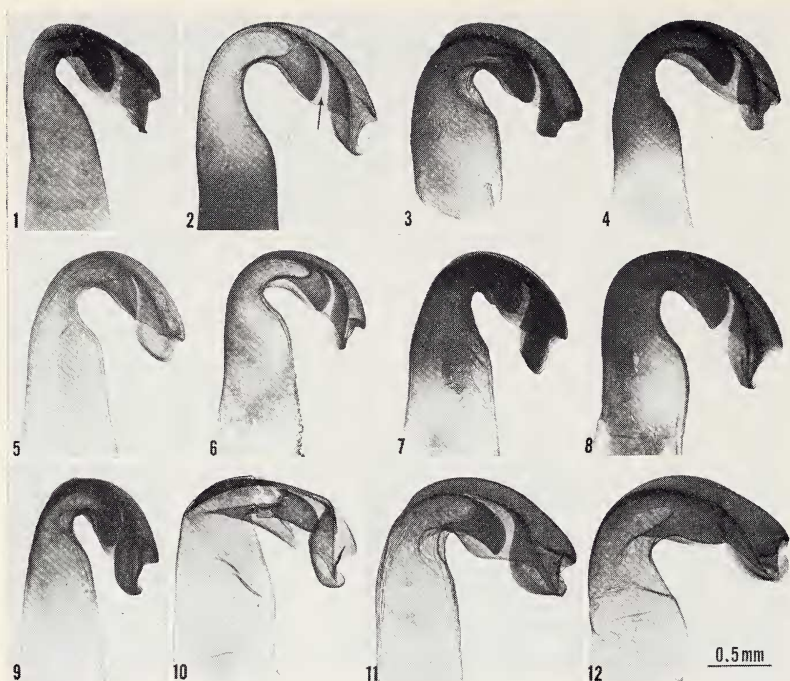
RESULTS AND DISCUSSION

The male genitalia of *Blaberidae* consist of 3 main structures (McKittrick's, 1964 terminology). The right phallomere (R2) (Figs. 1-12) is a retractable hook, and all the species have a sub-apical incision (Fig. 2, arrow). The median sclerite (L2vm) is solidly attached (in *Blaberus* spp.) to L2d (L2 dorsal = the virga, penis, or aedeagus) (Fig. 52). The prepuce (mantle of Hebard's, 1917 terminology) is a soft, flexible membrane (Fig. 52) bearing characteristic spines, or truncate or rounded sclerotized elevations. The left side of the prepuce is solidly attached by sclerotization to the side of the L2 phallomere, whereas the right side is usually connected by a flexible membrane which permits it to fold partly around the virga. One of the sclerites (L1) (Figs. 13-24) of the left phallomere in all the species of *Blaberus* studied are more or less similar and have a heavily sclerotized cleft, noted by McKittrick (1964).

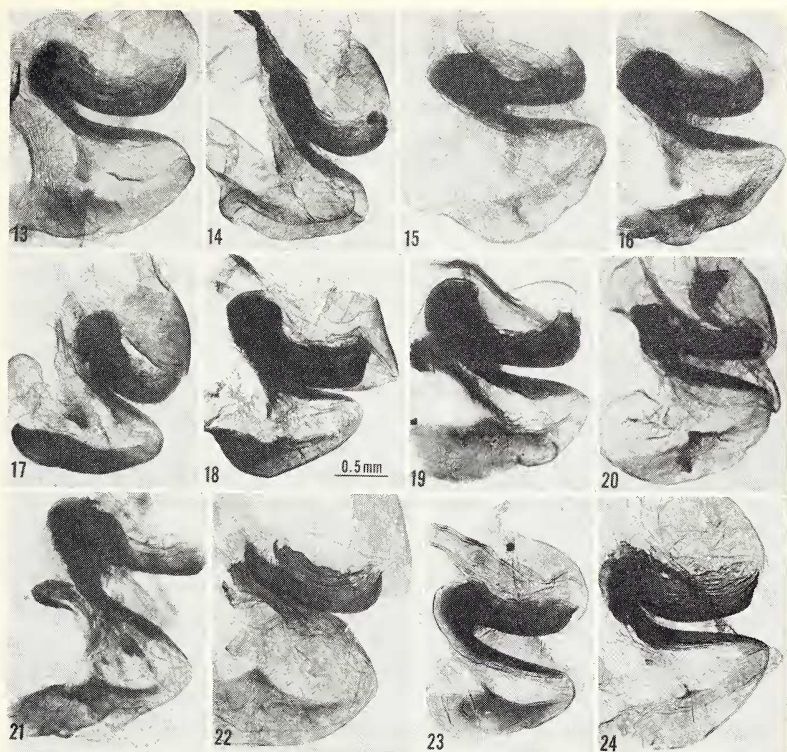
Based on body size, color, and shape of the pronotum, Hebard (1931) placed *fusiformis*, *brasilianus*, *anisitsi*, and *scutatus* in the *Brasilianus* Group of the genus. Princis (1946) divided 8 species into the *Giganteus* and *Atropos* Groups, basing his divisions on the shape of L2d and the spines present on the prepuce. He did not examine the genitalia of *minor*, *brasilianus*, *fusiformis*, and *scutatus*, but suggested that the *Brasilianus* Group, established by Hebard, probably should be included in the *Atropos* Group. As a result of my examination of the 4 species not investigated by Princis, I believe Hebard was correct in erecting the *Brasilianus* Group and I place the above 4 species in this group.

Species of *Blaberus* can be readily placed in their respective Groups, by the shape of the virga and preputial spines. However, variation is such that specific determination is often difficult. The 3 *Blaberus* Groups may be distinguished in the following key:

1. L2d recurved dorsally and slightly to the right, usually forming a hooklike structure (Fig. 52). Extending dorsally and laterally on the left, about where L2vm and L2d are solidly joined, is a sclerotized tumorlike outgrowth (Fig. 52, T). There are no large truncate elevations and all of the spines on the preputial membrane are relatively small (Figs. 28-40, 47-57, 62-74, 215) *Giganteus* Group.
- L2d not hookshaped. Tumorlike outgrowth on the left side absent. Prepuc with anterior truncate or rounded elevations almost always present on the left, and sometimes on the right side of the preputial membrane 2.



Figs. 1-12. Right hooked phallomere (R2) of *Blaberus* spp. 1-2. *Giganteus* Group. 1. *B. craniifer*. (ANSP), Juxtlahuaca Cave, Colotlipa, Mexico (det. as *B. trapezoideus* by Rehn). 2. *B. giganteus*. (ANSP), Muzo, Colombia (arrow indicates the subapical incision). 3-6. *Brasilianus* Group. 3. *B. scutatus*. (ANSP), Ceara Mirim, Rio Grande do Norte, Brazil. 4. *B. fusiformis*. (ANSP), Provincia Sara, Dept Vera Cruz, Bolivia. 5. *B. brasilianus*. (ANSP), Natal, Brazil. 6. *B. minor*. (ANSP), Mission Tacaagl , Formosa, Argentina (det. Hebard). 7-10. *Atropos* Group. 7. *B. atropos*. (MCZ), Mexico. 8. *B. parabolicus*. (N), Ecuador. 9. *B. discoidalis*. (N), Panama. 10. *B. boliviensis*. (L), Guayaquil, Ecuador (det. Princis). 11-12. *Brasilianus* Group. 11. *B. colosseus*. (ANSP), Fyzabad, Trinidad. 12. *B. sp. D* (probably *colosseus*). (ANSP), St. Laurent du Maroni, French Guiana (from specimen shown in Fig. 208). (all to scale shown in Fig. 12).



Figs. 13-24. Left phallomere (L1) of *Blaberus* spp. 13-14. *Giganteus* Group. 13. *B. giganteus*. (ANSP), Muzo, Colombia. 14. *B. craniifer* (ANSP), Juxtlahuaca Cave, Colotlipa, Mexico (det. as *B. trapezoideus* by Rehn). 15-18, 22. *Brasilianus* Group. 15. *B. brasilianus*. (ANSP), Natal, Brazil. 16. *B. scutatus*. (ANSP), Ceara Mirim, Rio Grande do Norte, Brazil. 17. *B. minor*. (ANSP), Villa Ana F.C.S.F., Argentine Republic (det. Hebard). 18. *B. fusiformis*. (ANSP), Santa Cruz de la Sierra, Bolivia (det. Hebard). 19-21, 23, 24. *Atropus* Group. 19. *B. parabolicus*. (N), Ecuador. 20. *B. discoidalis* (N), Panama. 21. *B. atropus*. (N), Trinidad. 22. *B. colosseus*. (ANSP), Caparo, Trinidad (det. Hebard). 23. *B. anisitsi*. (L), (det. Princis). 24. *B. boliviensis*. (L), Guayaquil, Ecuador (det. Princis). (all to scale shown in Fig. 18).

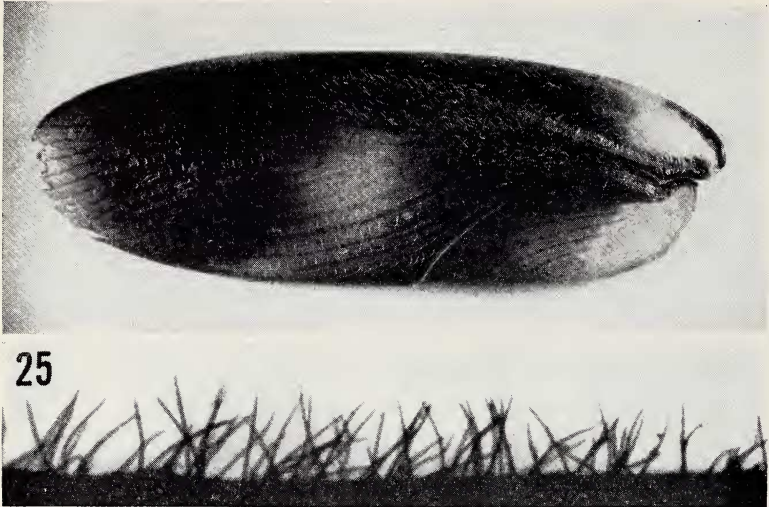
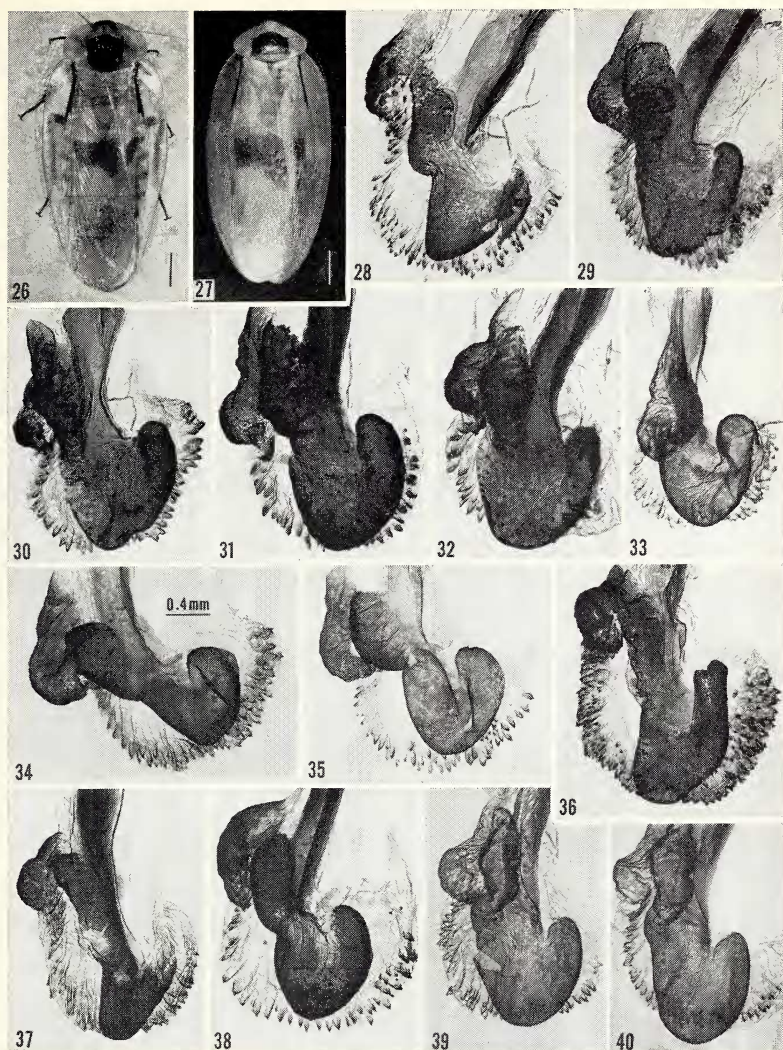
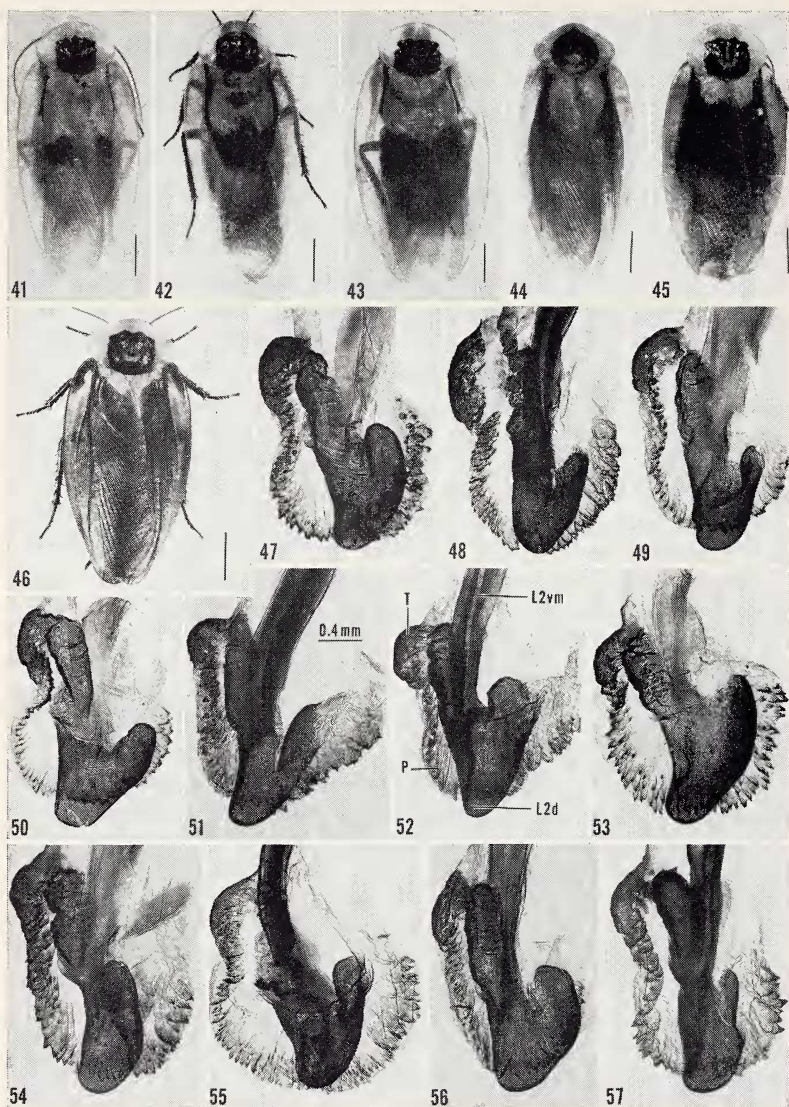


Fig. 25. Upper. Tegmen of *B. craniifer* showing the distribution of the long setae on the marginal and scapular fields. Lower. Anterior view of part of the tegmen showing the characteristic hairlike setae.

2. Anterior elevations usually rounded, present on the left and often on the right sides. Differences in size between anterior elevations on the right and left sides not great. Preputial spines numerous, usually on the left and right sides and often occur in more than a single row (Figs. 76, 77, 79-82, 84-91, 93-111, 211-214). In *colosseus* the left preputial spines usually occur in a single row (Figs. 116-129) *Brasilianus* Group.
- Truncate or rounded elevations usually present only on the left side and generally much larger and more robust than spines on the right. Preputial spines usually less numerous than in the *Brasilianus* Group, and are often arranged (when present) in a single row on the left, and single or sometimes double or partial double row on the right. Spines on the right side usually more numerous than on the left (Figs. 133-153, 155-170, 174-198, 200, 201, 203, 204, 210) *Atropos* Group.
- Giganteus* Group. — Two species of *Blaberus* (*giganteus*, Figs. 26, 27; *craniifer*, Figs. 41-46, 58-61) belong to this group. A useful tegminal character which Princis (1946) described can be used to distinguish *B. craniifer* from all other species of the genus. In *craniifer* the marginal field and scapular field of the tegmina have diffuse projecting hairs (Fig. 25). According to Princis, no other



Figs. 26-40. *B. giganteus* (*Giganteus* Group). 26. (N). 27. (USNM), St. Jean, French Guiana (det. as *B. colosseus* by Hebard) (scale = 10 mm). 28-40. L2d and prepuce (all to scale shown in Fig. 34). 28. (USNM) (from specimen shown in Fig. 27). 29. (USNM), Cabima, Panama. 30. (USNM), Ft. Clayton, Canal Zone. 31. (AMNH), Barro Colorado Island, Canal Zone. 32. (USNM), Chilibrillo Cave, Buenos Aires, Canal Zone. 33. (USNM), Puerto Berrio, Colombia. 34-35. (ANSP), Muzo, Colombia. 36. (USNM), Atlantico, Colombia. 37. (AMNH), Colombia. 38. (AMNH), Caripito, Venezuela. 39-40. (N).



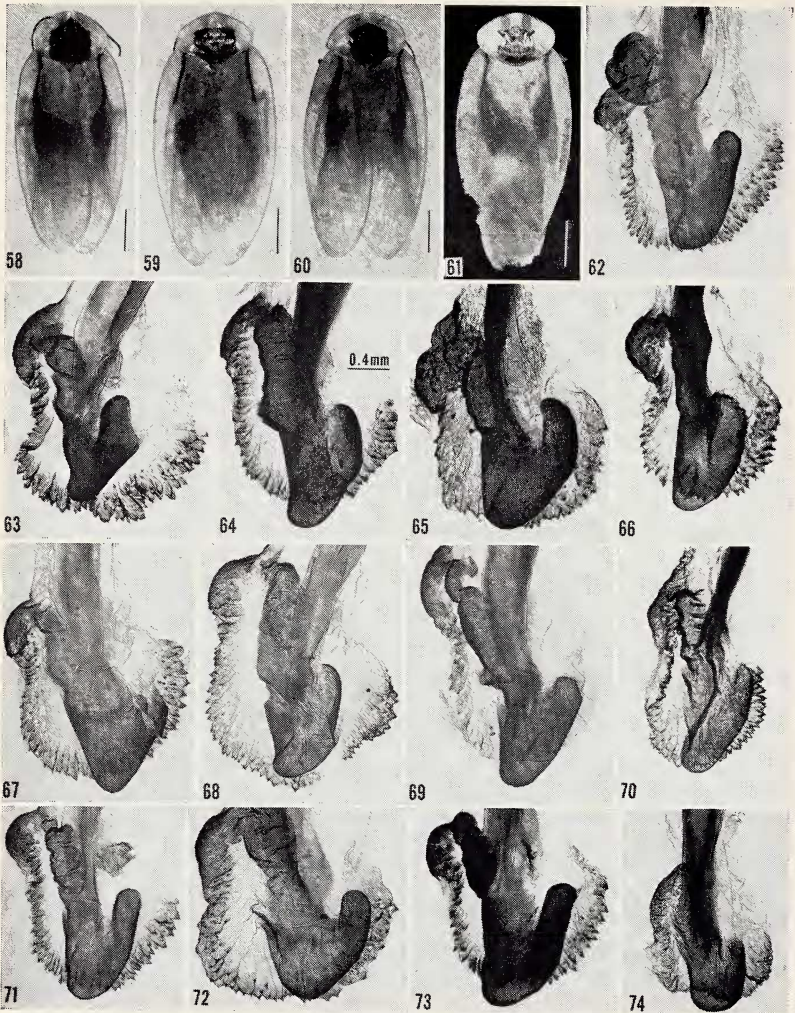
Figs. 41-57. *B. craniifer* (*Giganteus* Group). 41-46. Adult males (scale = 10 mm). 41. (USNM), Cordoba, Mexico (det. as *B. trapezoides* by Rehn). 42. (N). 43. (USNM), Rancho Qemado, Rt. 85, Mexico. 44. (USNM), Teapa, Tabasco, Mexico. 45. (USNM), Key West, Florida. 46. (N). 47-57. L2d and prepuce (all to scale shown in Fig. 51). 47. (USNM), Mexico (from specimen shown in Fig. 41). 48. (USNM), Mexico

Blaberus has this character, although I have seen a few very minute hairs in some specimens of *B. giganteus*.

In *craniifer* the tumorlike sclerotized outgrowth on the left side of L2 extends caudally for a short distance and usually merges gradually into the border of the prepuce where small spines begin and form a fringe around the membrane. The sclerotized extension of the lateral outgrowth varies somewhat in length but is generally distinct (Figs. 47-51, 53-57, 62-64, 66-74). Exceptions are seen in Fig. 52 and 65. In *B. giganteus* there is usually little or no sclerotized extension from the tumorlike outgrowth into the preputial membrane, so that the preputial spines begin more abruptly at the outgrowth (Figs. 28-35, 38-40). Exceptions to this are shown in Fig. 36 and 37. In both species the preputial spines may occur in more than a single row, and in some individuals there may be a reduction in the number of preputial spines (Figs. 37, 65, 70, 74).

If Princis' (1946) tegminal character is valid for *B. craniifer* then I have not seen any correctly determined specimens of *B. trapezoideus*. All the specimens determined by Hebard or Rehn as *trapezoideus* (Figs. 41, 58-61) have hairy tegmina and I therefore consider them to be light forms of *B. craniifer*. The genitalia of these "*trapezoideus*" (e.g., Figs. 47, 63, 64, 66) are indistinguishable from *craniifer*. Two specimens identified as *B. trapezoideus*, received from the University Zoological Museum, Copenhagen, Denmark were actually *B. craniifer* (Costa Rica) and *B. parabolicus* (Peru). According to Princis (1946) the preputial spines of *trapezoideus* are similar to *giganteus* but are smaller and more numerous, though always clearly separated from each other. Considering the variation in size, number, and spacing of preputial spines I doubt if this character can be used to distinguish *trapezoideus* from *giganteus*. Princis also (1958) states that the pronotum of *trapezoideus* is laterally truncated with approximately parallel sides. Some individuals of our light-phased form of *craniifer* (in culture) (Fig. 42) also have the pronotum laterally truncate. It is possible that *trapezoideus* and *craniifer* are simply variants of the same species. The type localities of the 2 spp. of the

(from specimen shown in Fig. 43). 49. (USNM), Vera Cruz, Mexico. 50. (USNM), Tuxtepec, Oaxaca, Mexico (labelled *trapezoideus*). 51. (USNM), Mexico (from specimen shown in Fig. 44). 52. (MCZ), Chichén Itzá, Yucatan, Mexico. 53. (USNM), El Salvador. 54. (USNM), San Salvador, El Salvador. 55. (USNM), Benque Viejo, British Honduras. 56. (MCZ), Colón, Panama. (Abbreviations for Fig. 52. L2d = dorsal left phallomere; L2vm = ventromedial left sclerite (fused to L2d); P = prepuce; T = tumorlike outgrowth.)



Figs. 58-74. *B. craniifer* (*Giganteus* Group). 58-61. Adult males (scale = 10 mm). 58. (ANSP), Guatemala. 59. (ANSP), Vera Cruz, Mexico. 60. (ANSP). 61. (ANSP), Juxtlahuaca Cave, Colotlipa, Mexico. (These 4 males were determined as *B. trapezoideus* by Rehn, or Hebard.) 62. (MCZ), Havana, Cuba (det. Rehn). 63. (USNM), Santiago-Vegas, Cuba. 64. (ANSP) (from specimen shown in Fig. 60). 65. (AMNH), Turrialba, Costa Rica. 66. (ANSP) (from specimen shown in Fig. 61). 67. (MCZ), Havana, Cuba. 68-69. (MCZ), Colón, Panama. 70. (N). 71. (MCZ). 72. (ANSP), San Miguel, Vera Paz, Guatemala (det. as *B. colosseus* by Hebard). 73. (USNM), Florida (from specimen shown in Fig. 45). 74. (N).

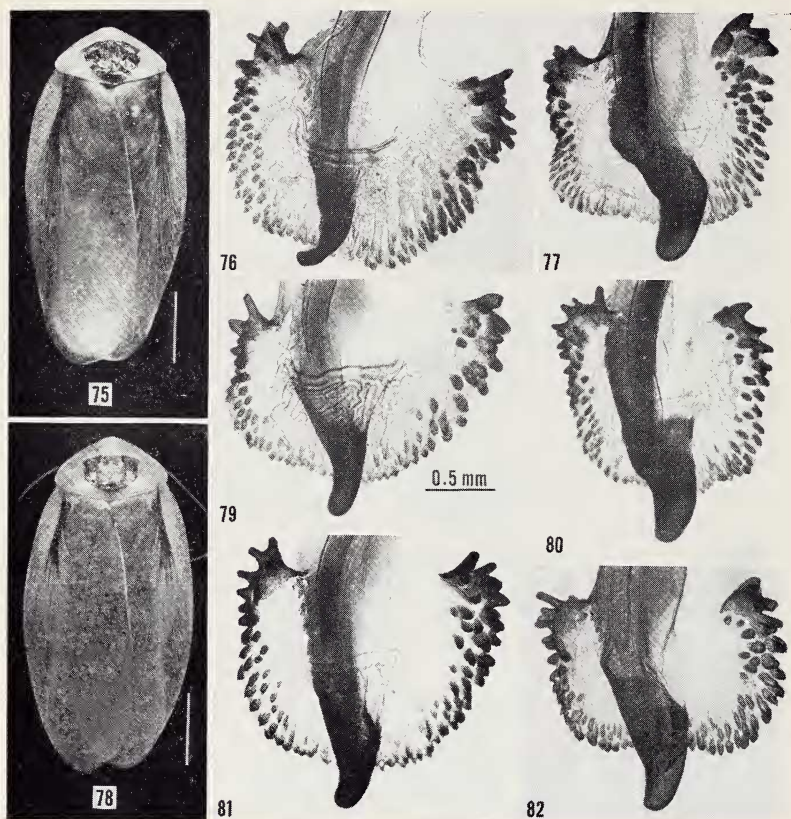
Giganteus Group are: *giganteus* — "America"; *craniifer* — Cuba. (see addendum regarding *trapezoideus*).

Although color markings are variable in several species of *Blaberus*, they are especially so in *B. craniifer*. This species is represented by light (Figs. 41-43) and dark (Figs. 45, 46) forms with intermediates (Fig. 44) connecting the extremes. Markings of light phased individuals resemble *B. giganteus* (cf. Figs. 26, 27). Lefeuvre (1960) has described some color varieties which occurred in his laboratory culture of *craniifer* and we have cultures of both light and dark forms which crossed successfully. Lefeuvre claims that rearing *craniifer* for a number of years favored the formation of an "artificial subspecies" which differed from the original in 1) coloration of the pronotum, 2) general coloration, in particular the male, and 3) the morphology of the penis and prepuce. Lefeuvre suggested that the original *B. craniifer* may have hybridized with a closely related species. The variations in *craniifer* which Lefeuvre described can be seen in museum specimens from different geographic localities. I have never seen any dark forms of *B. giganteus* comparable to dark *craniifer*.

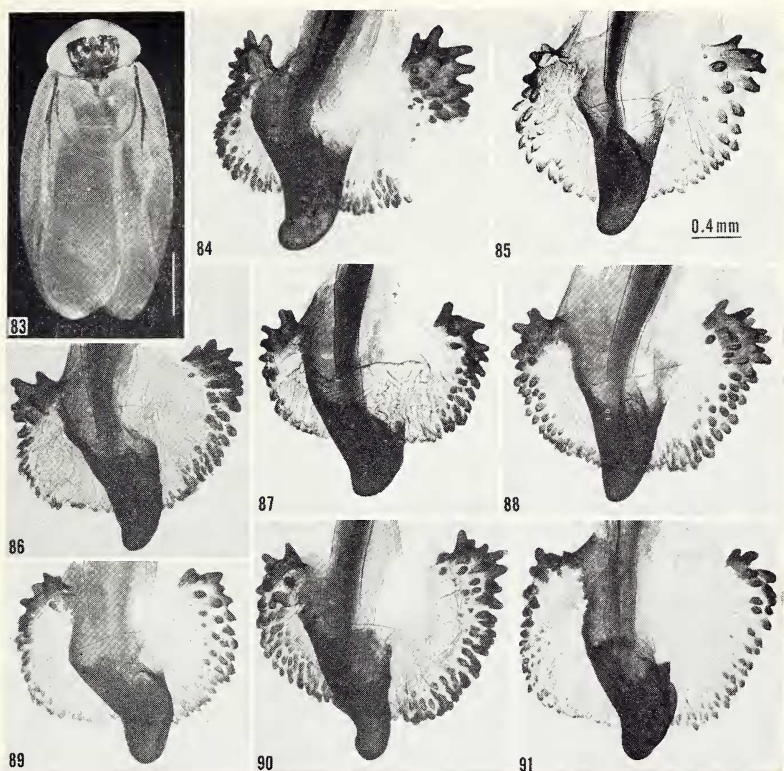
Brasilianus Group. — The 5 species in this Group, namely, *scutatus* (Fig. 75), *brasilianus* (Fig. 78), *fusiformis* (Fig. 83), *minor* (Fig. 92), and *colosseus* (Figs. 112-115), show some genitalic differences in L2d and preputial spines but variation is so great within 4 of these species (Figs. 76, 77, 79-82, 84-91, 93-111), that specific determinations, using genitalia alone, are often impossible. In some individuals of *fusiformis* (Figs. 85-87, 89, 91) and *minor* (Figs. 94-95, 100, 106) there is a marked reduction or loss of preputial spines and they may occur in a single row, usually on the left side.

Characteristic of this group is the anterior elevations which are generally fused on the right side, and are about the same size as those on the left. Rarely are the anterior spines on the right larger than those on the left (e.g., Figs. 84, 85, 88). The preputial spines decrease only slightly in size from the anterior to posterior position. When the spines are numerous and occur in more than a single row they are often closely spaced and form a more or less dense uniform fringe around the preputial membrane (e.g., Figs. 76, 77, 79-82, 88, 90, 93, 97, 99, 101, 105).

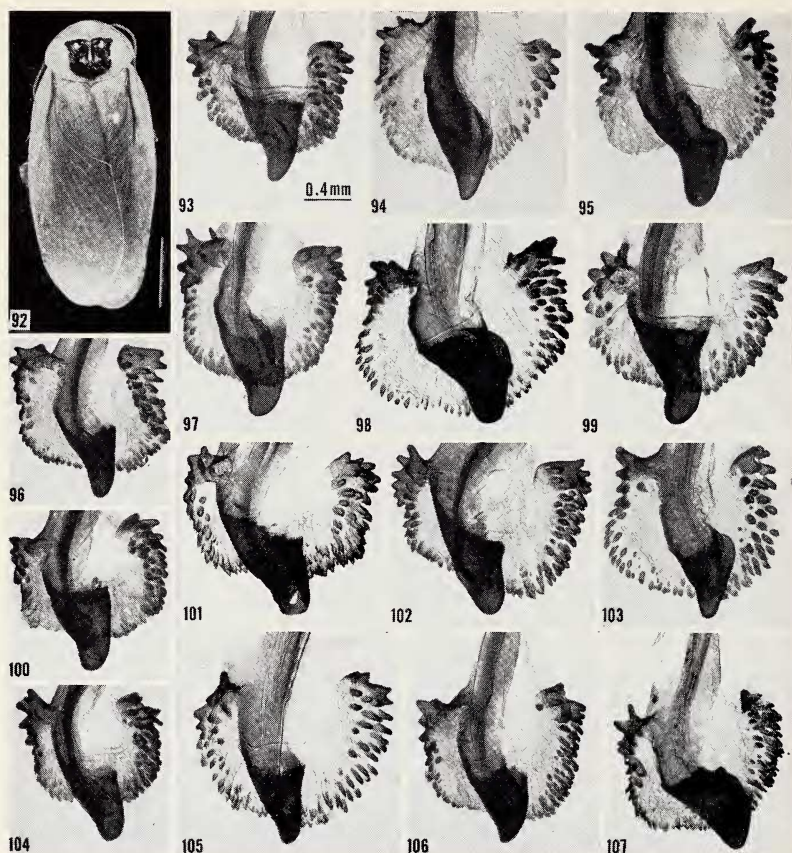
Hebard (1921, p. 148) stated, "From a study of the material in the Philadelphia collections, as well as specimens recently received from the Guianas, we are finally convinced that *B. colosseus* (Illiger) was based on a mere individual variation of *giganteus*, unworthy of nominal recognition." Princis (1963) followed Hebard and listed



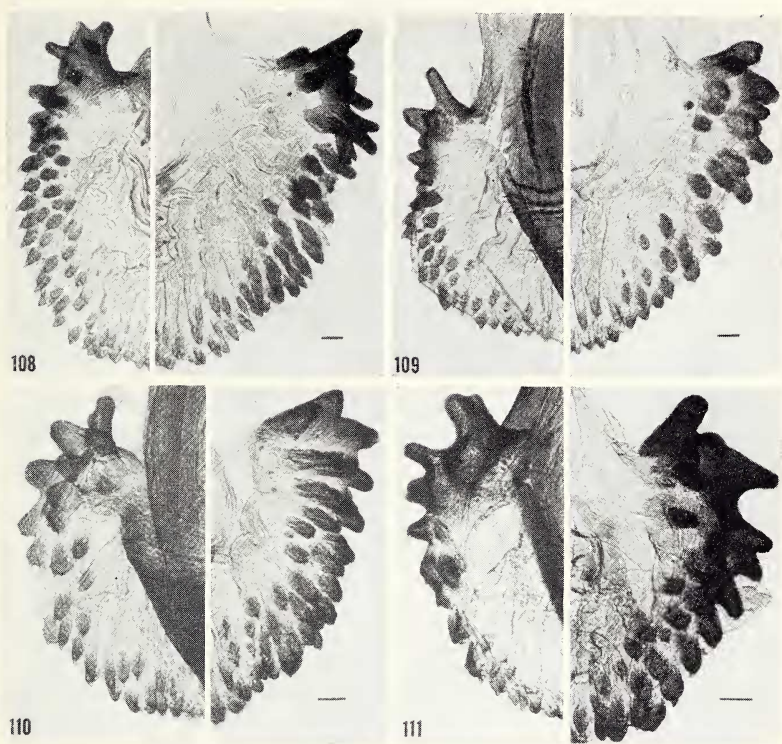
Figs. 75-82. *Brasilianus* Group. 75-77. *B. scutatus*. 75-76. (ANSP), Pernambuco, Brazil (paratype of *B. scutata* var. *obscura* S. and Z.). 77. (ANSP), Ceara Mirim, Rio Grande do Norte, Brazil. 78-82. *B. brasilianus*. 78-79. (ANSP), Natal, Brazil. 80. (ANSP), Independencia, Parahybo, Brazil. 81. (MCZ), Brazil. 82. (USNM), Natal, Brazil. (Scale for adults = 10 mm; all genitalia to scale shown in Fig. 79.)



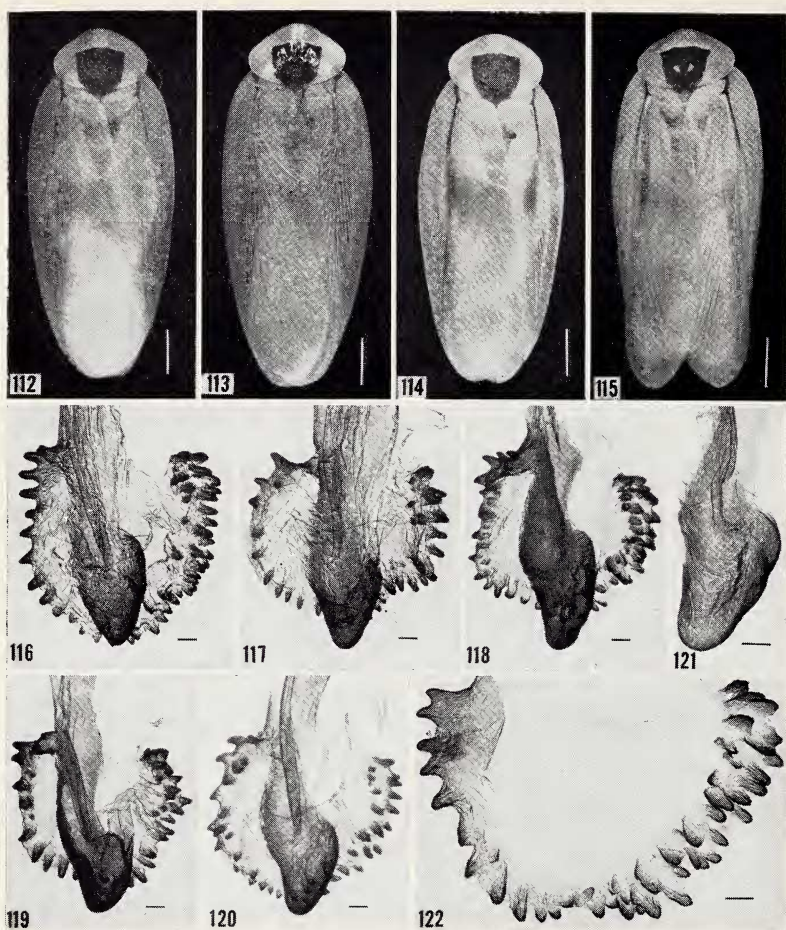
Figs. 83-91. *B. fusiformis* (*Brasilianus* Group). 83. Adult male (scale = 10 mm). (ANSP), Santa Cruz de la Sierra, Bolivia (det. Hebard). 84-91. L2d and prepuce (all to scale shown in Fig. 85). 84. (ANSP), Carumbo, Matto Grosso, Brazil (a portion of the prepuce on the right side is missing). 85. (ANSP), San Francisco, Argentina. 86. (ANSP), Provincia Sara, Dept. Vera Cruz, Bolivia (det. Hebard). 87. (ANSP), Bolivia (from specimen shown in Fig. 83). 88. (ANSP), Provincia Sara, Dept. Vera Cruz, Bolivia. 89. (ANSP), Jundiahy, Brazil. 90. (USNM), Utiariti Rio, Matto Grosso, Brazil. 91. (ANSP).



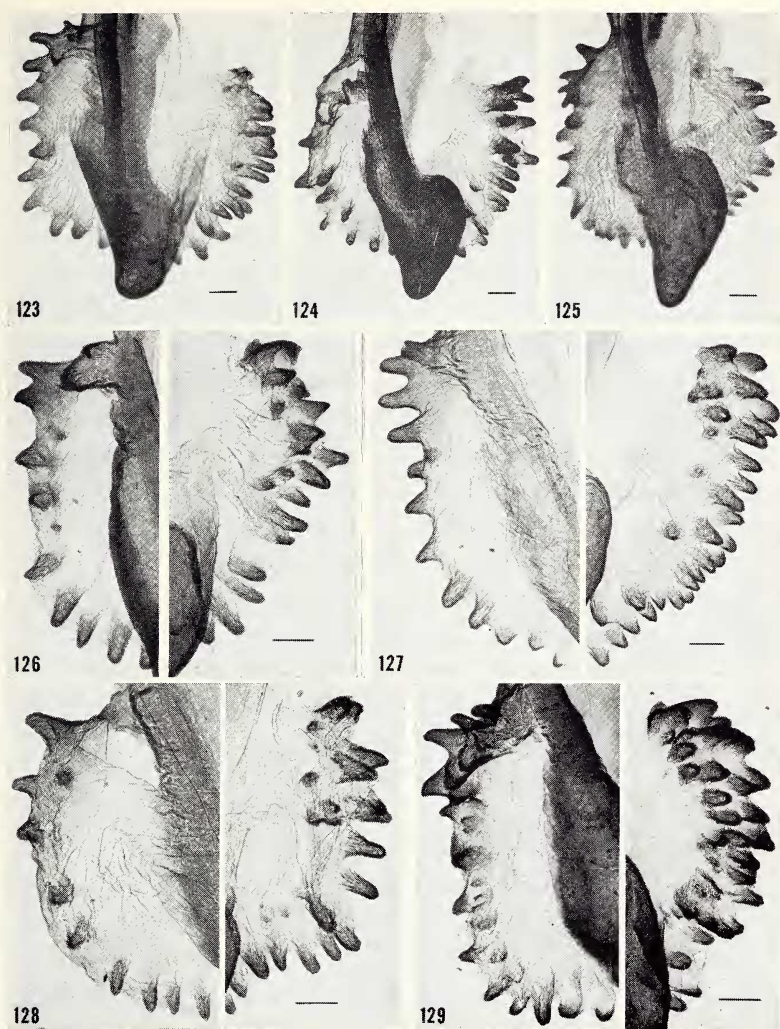
Figs. 92-107. *B. minor* (*Brasilianus* Group). 92. Adult male (scale = 10 mm). (ANSP), Argentina (det. Hebard). 93-107. L2d and prepucal (all to scale shown in Fig. 93). 93. (ANSP), Paraguay. 94. (USNM), Natal, Brazil. 95. (USNM), Brooklin, São Paulo, Brazil. 96. (ANSP), Mission Tacaaglé, Formosa, Argentina. 97-98. (ANSP), Formosa, Argentina. 99. (ANSP), Argentina (from specimen shown in Fig. 92). 100-102. (ANSP), Chaco del Santiago del Estero Bords du Rio Selado Environs D'Icaño, Argentina. 103. (ANSP), Formosa, Argentina. 104. (ANSP). 105. (ANSP), Chaco de Santiago del Estero Rio Salado, Argentina. 106-107. (ANSP), Gran Chaco, Argentina.



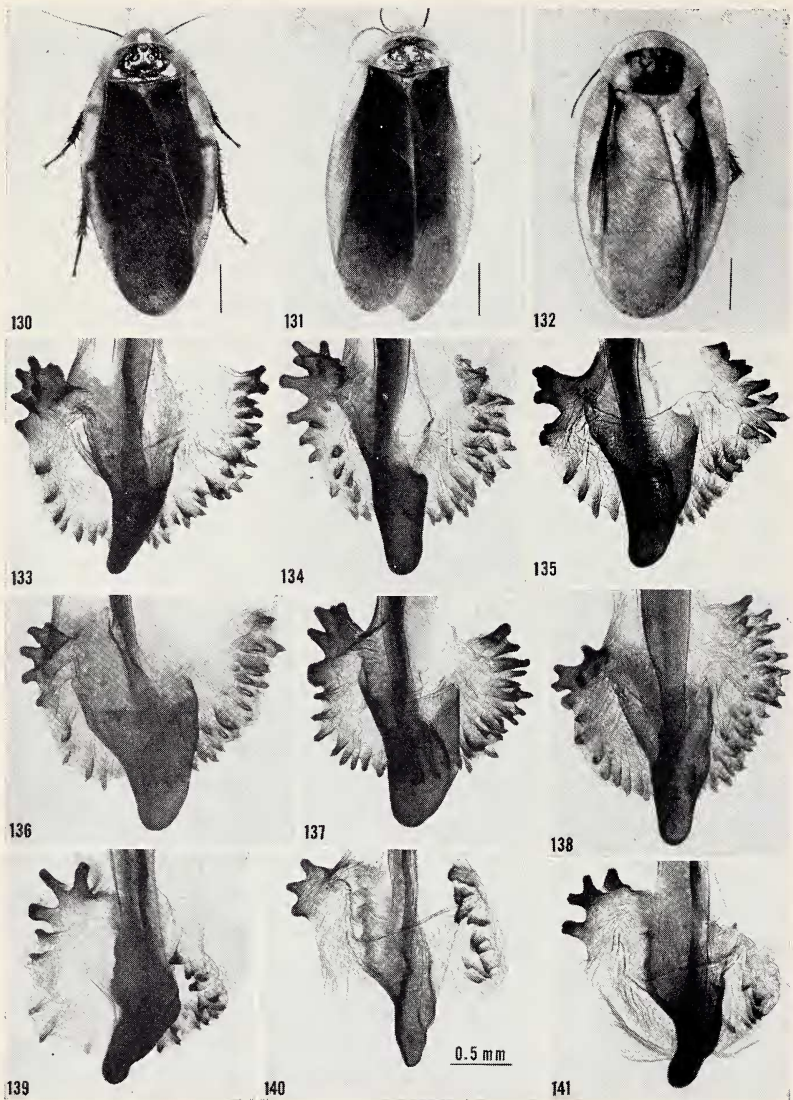
Figs. 108-111. *Brasilianus* Group. Right and left sides of the prepuce. 108. *B. scutatus* (from Fig. 76). 109. *B. brasilianus* (from Fig. 79). 110. *B. minor* (from Fig. 99). 111. *B. fusiformis* (from Fig. 87). (scale = 0.1 mm).



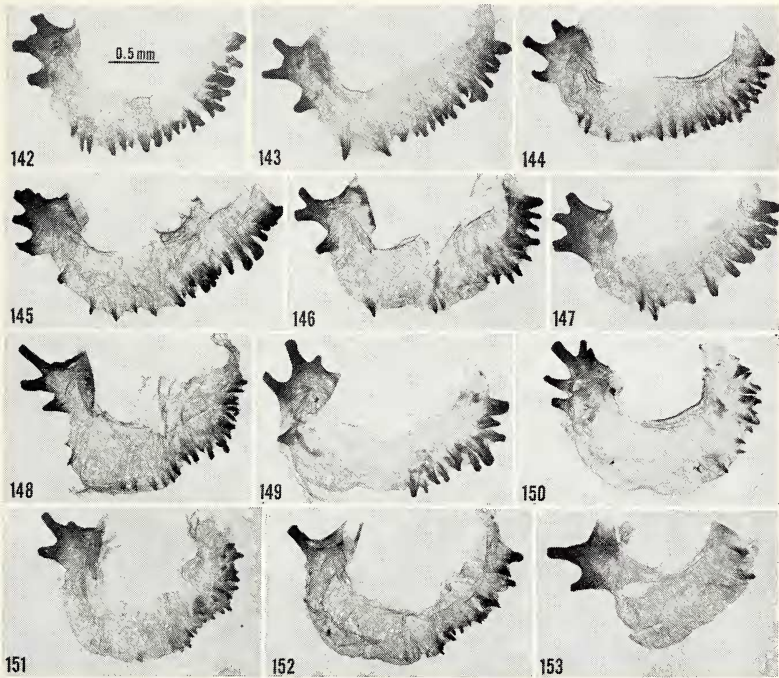
Figs. 112-122. *B. colosseus* (*Brasilianus* Group). 112-115. Adult males (scale = 10 mm). 112. (ANSP), Caparo, Trinidad. (This specimen is Fig. 4 in Hebard, 1916.) 113. (ANSP), Fyzabad, Trinidad. 114. (ANSP), Caparo, Trinidad. (This specimen is Fig. 5 in Hebard, 1916.) 115. (MCZ), Mexico. 116-122. L2d and prepuce (scale = 0.2 mm). 116. (ANSP) (from specimen shown in Fig. 112). 117. (ANSP) (from specimen shown in Fig. 113). 118. (MCZ) (from specimen shown in Fig. 115). 119. (MCZ), Mexico. 120. (USNM), Trinidad. 121-122. (ANSP) (from specimen shown in Fig. 114; L2d and prepuce have been mounted separately).



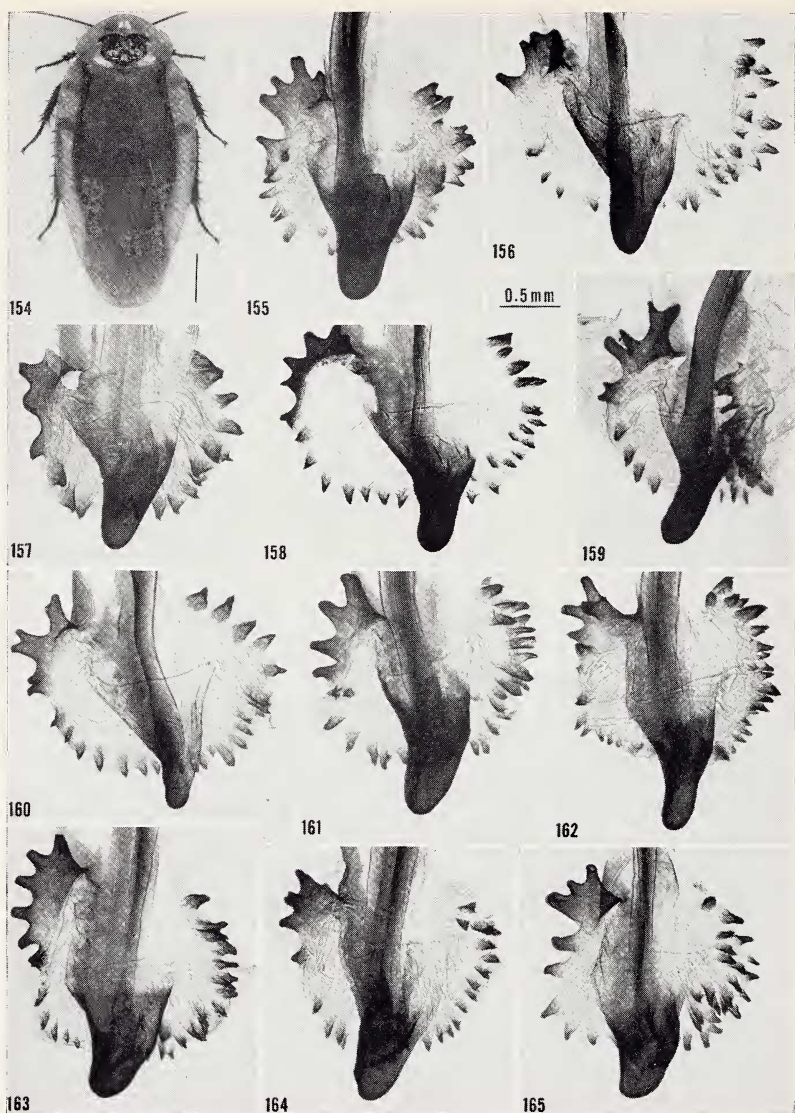
Figs. 123-129. *B. colosseus* (*Brasilianus* Group). 123. (AMNH), Trinidad. 124. (USNM), Trinidad (some of the anterior elevations on the left side are broken off). 125. (AMNH), Rancho Grande, near Maracay, Venezuela. 126-129. Right and left sides of the prepuce. 126. (MCZ) (from Fig. 119). 127. (ANSP) (from Fig. 116). 128. (ANSP) (from Fig. 117). 129. (MCZ) (from Fig. 118) (scale = 0.2 mm).



Figs. 130-141. *B. atropos* (*Atropos* Group). 130-132. Adult males (scale = 10 mm). 130. (N), Trinidad. 131. (MCZ), Mexico. 132. (USNM), Colombia (taken in quarantine on bananas at Charleston, S.C.). 133-141. L2d and prepuce (all to scale shown in Fig. 140). 133. (MCZ) (from specimen shown in Fig. 131). 134. (USNM) (from specimen shown in Fig. 132). 135. (USNM), Georgetown, British Guiana. 136-138. (USNM), Trinidad. 139-141. (N), Trinidad.



Figs. 142-153. Prepuce of *B. atropos*. From Natick culture which originated in Trinidad (all to scale shown in Fig. 142).



Figs. 154-165. *B. parabolicus* (*Atropos* Group). 154. Adult male. (N), Puraquequara, Rio Negro, Amazonas, Brazil (scale = 10 mm). 155-165. L2d and prepuce (all to scale shown in Fig. 158). 155. (AMNH), Colombia. 156. (MCZ), Napo or Marañon (Ecuador or Peru, northern Andes). (Type specimen of *Blaber armigera* Scudder.) 157. (MCZ), Upper Amazon? 158. (USNM), Gavião, Rio Negro, Amazonas, Brazil. 159. (N), Ecuador.

Blaberus colosseus as a synonym of *B. giganteus*. However, Hebard (1916, p. 292) described the prepuce of *colosseus* as follows: "... The surrounding mantle having the free dorsal and distal margins fringed with small blunt chitinous projections, these longer and more like short blunt teeth of a comb on the sinistral margin." This description does not fit a member of the *Giganteus* Group. I have examined the male genitalia of several specimens including some which Hebard used in his study and conclude that *colosseus* is not *giganteus*. The genitalia of *colosseus* (Figs. 116-129) differs markedly from that of *giganteus* (Figs. 28-40). *B. colosseus* phenotypically resembles *giganteus*, but it is paler in color (Hebard 1916); it is the largest member of the *Brasilianus* Group, and the only species in this group which in size, color, and markings (some individuals) resembles *B. giganteus*.

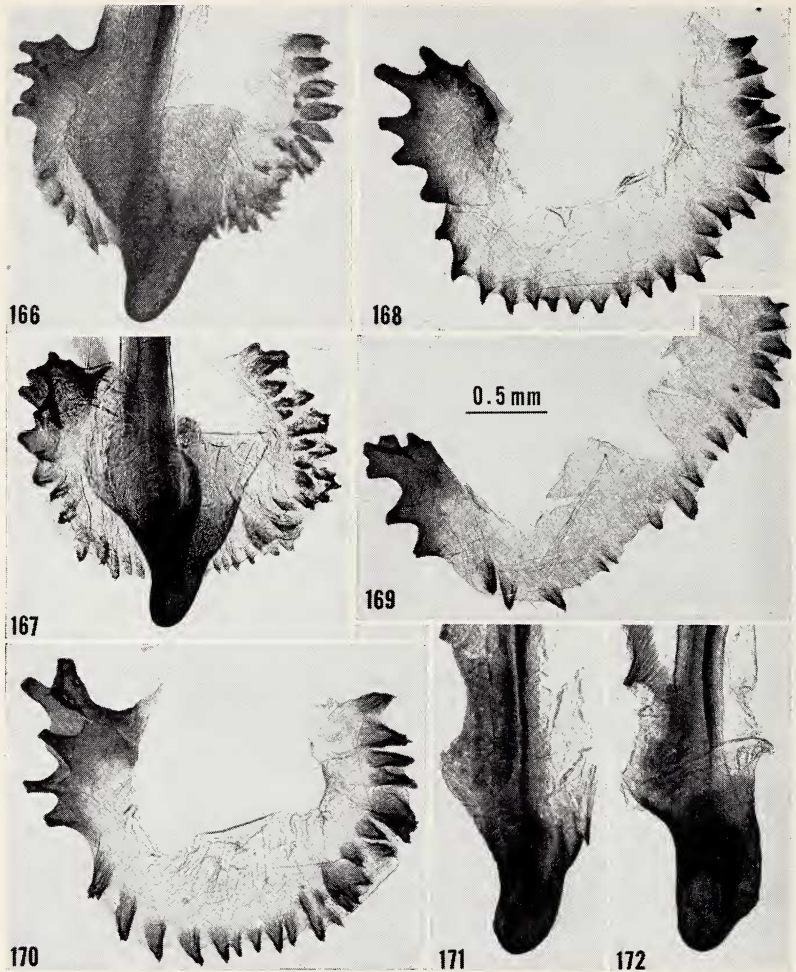
The prepuce of *colosseus* combines features of both the *Brasilianus* and *Atropos* Groups. The relatively small anterior elevations on the left side of the prepuce are not much larger than the spines on the right (Figs. 116-120, 122-129) a characteristic of the *Brasilianus* Group. However, the preputial spines of *colosseus* are all relatively large, fairly widely separated, particularly on the left side, and resemble these spines in the *Atropos* Group. With few exceptions (Figs. 184, 188) species of the *Atropos* Group have anterior truncate or rounded elevations on the left side of the prepuce that are much larger and more robust than the spines on the right side (Figs. 133-153, 155-170, 174-183, 185-187, 189-198, 200, 201, 203, 204, 210).

One specimen from Guatemala, determined as *B. colosseus* by Hebard is actually *Blaberus craniifer* (Fig. 72). Two specimens (ex Canal Zone and French Guiana) determined by Hebard as *colosseus* are *giganteus* (Figs. 27, 28). The specimens which Hebard claimed were *colosseus* came from Trinidad, Guatemala, Costa Rica, and Panama. I have seen 9 specimens of *colosseus*; 6 were from Trinidad, 2 from Mexico, and 1 from Venezuela. One specimen from French Guiana is probably *colosseus* (Figs. 208, 214). The distribution of this species must await an examination of additional material.

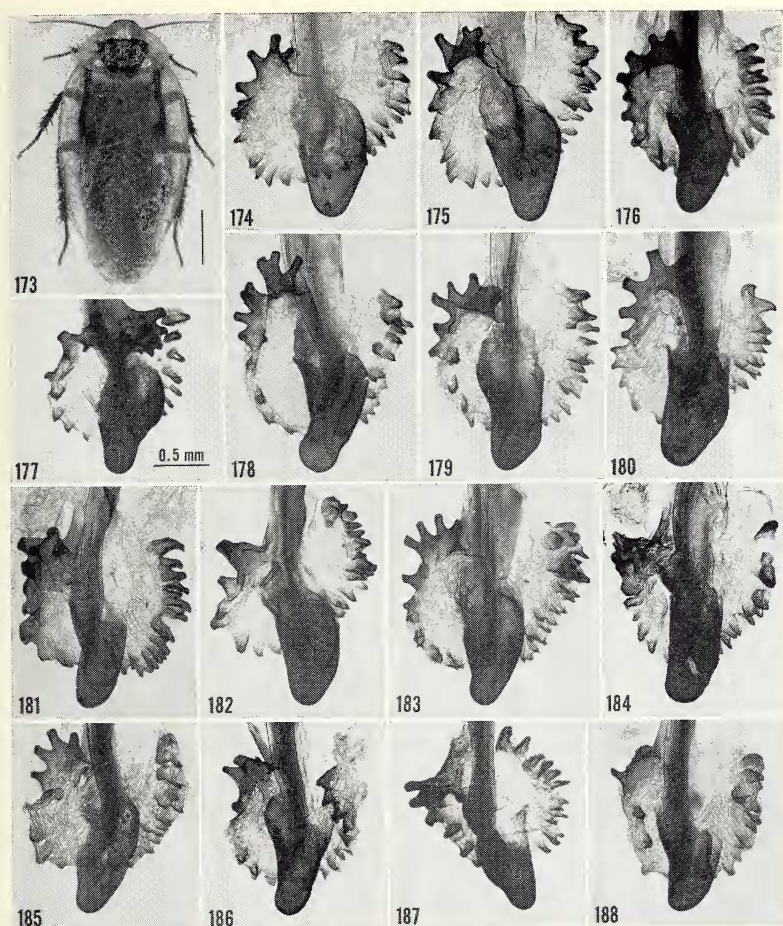
Atropos Group. — Five species, *atropos* (Figs. 130-132), *parabolicus* (Fig. 154), *discoidalis* (Fig. 173), *boliviensis* (Fig. 199), and *anisitsi* (Fig. 202) belong to this group.

The armament on the preputial membrane shows the greatest varia-

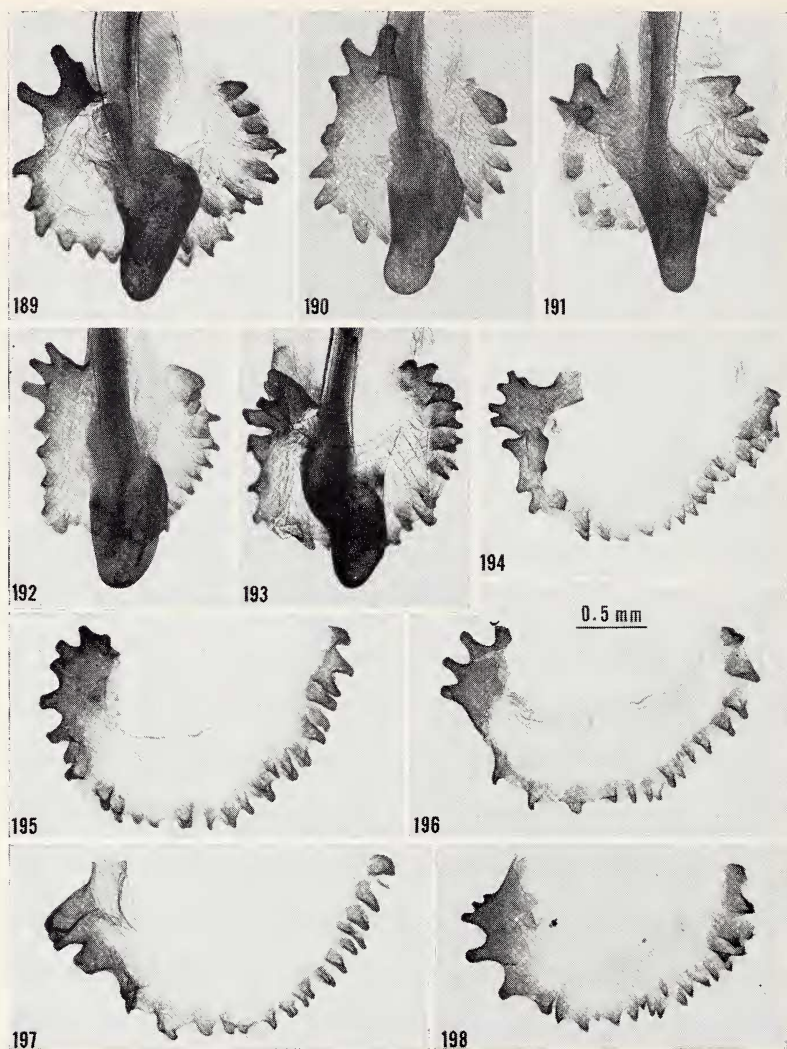
160. (N), Borba, Rio Madeira, Amazonas, Brazil. 161. (AMNH), Iquitos, Peru. 162. (AMNH), Rio Ucayali, Peru. 163. (AMNH), Moyobamoa, San Martin, Peru. 164. (AMNH), Rio Ucayali, Peru. 165. (AMNH), Rio Maraion, Peru.



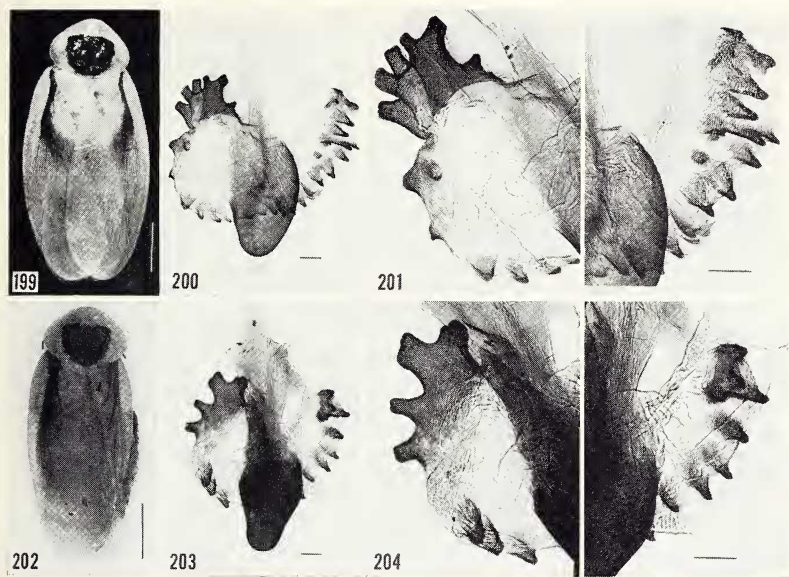
Figs. 166-172. *B. parabolicus* (*Atropos* Group). L2d and prepuce. The two structures have been mounted separately in Figs. 168-172 (all to scale shown in Fig. 169). 166-167. (USNM), South America. 168-172. (N), Puraquequara, Rio Negro, Amazonas, Brazil.



Figs. 173-188. *B. discoidalis* (*Atropos* Group). 173. Adult male (scale = 10 mm). (N), Panama. 174-188. L2d and prepuce (all to scale shown in Fig. 177). 174-175. (MCZ), Nicaragua. 176-177. (N), Panama. 178. (USNM), Pontarenas, Costa Rica. 179. (MCZ), Trinidad. 180. (AMNH), Colombia. 181. (USNM), Trinidad. 182. (MCZ), Panama. 183. (AMNH), Barro Colorado, Canal Zone, Panama. 184. (USNM), Colombia (from wild orchids at Hoboken Quarantine). 185. (AMNH), Barro Colorado, Canal Zone, Panama. 186. (USNM), British Guiana. 187. (N), Panama. 188. (AMNH), Puerto Plata, Dominican Republic.



Figs. 189-198. *B. discoidalis* (*Atropos* Group). L2d and prepuce; in 194-198, L2d has been removed (all to scale shown in Fig. 196). 189. (USNM), Ecuador. 190. (USNM), Venezuela. 191. (AMNH), Colombia. 192. (AMNH), labeled "Africa" which is undoubtedly an error. 193-197. (N), Panama. 198. (MCZ).



Figs. 199-204. *Blaberus* spp. (*Atropos* Group). Genitalia from the adult specimens shown. 199-201. *B. boliviensis*. (L), Guayaquil, Ecuador (det. Princis). 202-204. *B. anisitsi*. (L) (det. Princis). Fig. 201 and 204 are enlargements of the preputial spines of the specimens shown in Fig. 200 and 203 (scale for adults = 10 mm, for genitalia = 0.2 mm).

tion in *atropos* (Figs. 133-153). Princis (1946) stated that the truncate elevation on the left side was 3-pronged whereas Hebard (1917) stated it was 2-pronged. These elevations may vary from a single arm (Fig. 152) to one consisting of more than 5 prongs (Figs. 133, 134). More striking is the marked reduction in numbers of the smaller preputial spines in some males. This usually occurs on the left side (Figs. 139-141, 144-153) where there are few spines to begin with but a marked reduction may occur even on the right side (Figs. 141, 153). In some males the spines are completely absent from the left side (Figs. 140, 141, 147, 149-153).

In *parabolicus* (Figs. 155-170) most of the spines on the right side of the prepuce are more or less pointed. In some males there is a reduction in number of spines (Figs. 156, 169). Bruijning (1959) described the genitalia of *parabolicus* as follows: "At the extreme right of the preputium stout, rounded processes are inserted between the teeth; some of the teeth on the free margin form pairs which are squarely inserted on the margin; sinistrad the teeth are developed in blunt, stout, chitinous processes, while at the extreme left a large bito trilobate process is found . . ." An examination of Figs. 155-170 shows that variability is so great that it is impossible to indicate specifically the number of truncate elevations on the left side or the exact arrangement and shapes of the preputial spines on the right.

In *B. discoidalis* (Figs. 174-198) the truncate elevations on the left usually arise very close to L2vm, extend dorsally, and may even overlap L2vm (Figs. 175-180, 190). Preputial spines are more numerous on the right side, usually are somewhat truncate but sometimes are rounded or pointed at the tips. In some specimens (Figs. 195, 198) the right anterior spines, though smaller, tend to resemble the large elevations of the left side except that they are rarely fused at their bases (Fig. 195). The spines decrease in size distally on the membrane and in some individuals there is a reduction in number, usually on the left side. L2d is variable in size and shape. In a few males the large truncate elevations which are highly variable in number on the left side are poorly defined or fused together (Figs. 182, 184, 188, 191) and sometimes (Fig. 184) are reminiscent of the tumorlike outgrowth on the left side in the *Giganteus* Group.

According to Princis (1946) the preputial armament is simple and sparse in *anisitsi* (Figs. 203, 204). His drawing shows a 3-pronged truncate elevation plus 3 bluntly rounded spines on the left side and only 5 smaller pointed spines on the right. The specimen shown in Fig. 203 was the one used by Princis (Fig. 6 in 1946; and identified

by him with reservations) but he did not remove the genitalia from the male; it differs from Princis' description in having a 4-pronged elevation on the left and more spines on the right (than he figured) terminating anteriorly in 3 spines fused at their bases (Fig. 204).

Hebard stated that the species related to *B. fusiformis* Walker ". . . are poorly understood and the description of *fusiformis* is vague. If our specimens are correctly determined it is possible that *anisitsi* is a synonym, based on material showing decided depauperation." Although Hebard included *anisitsi* in the *Brasilianus* Group, the specimen identified by Princis as *anisitsi* (Fig. 202) is clearly a member (by male genitalia, Fig. 203) of the *Atropos* Group (Princis 1946). If both Princis and Hebard are correct in their determinations *anisitsi* and *fusiformis* are obviously not the same species.

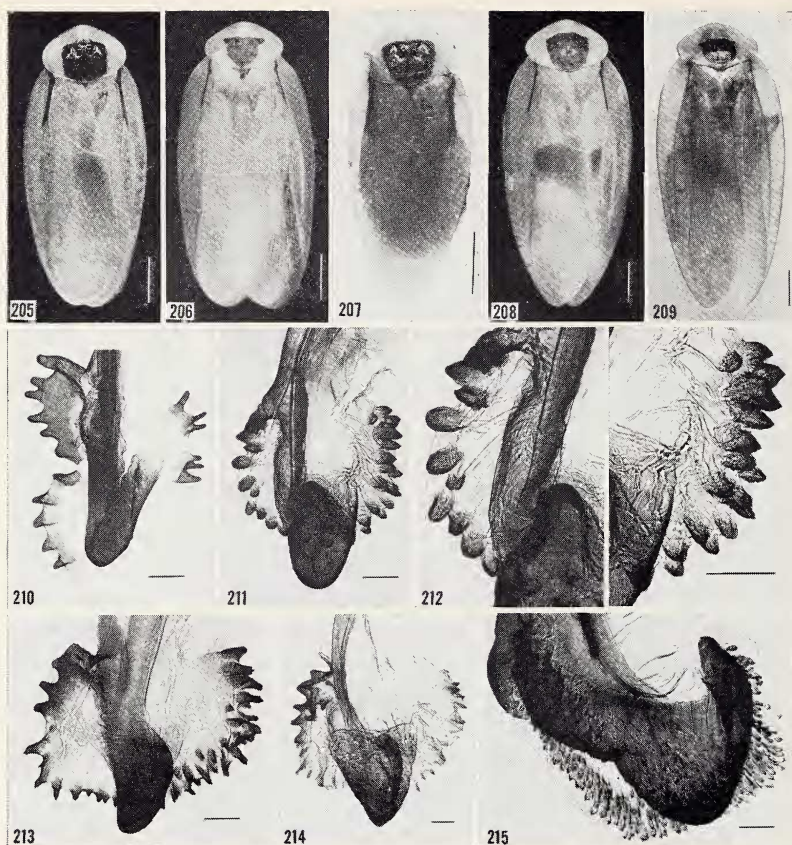
Princis (1946) compared the genitalia of *boliviensis* (Figs. 200, 201) with *anisitsi* (Figs. 203, 204). According to him the penis in *boliviensis* is more massive. The spines on the right side start with a bluntly rounded spine, are larger, more numerous and not as widely separated as in *anisitsi*. On the left side there is a 3-pronged truncate elevation followed by 10 (according to his drawing) truncate or rounded spines set fairly close together. In the specimen shown in Figs. 200, 201 (not the one illustrated by Princis), the truncate elevations on the left are at least 6-pronged. No doubt an examination of additional specimens of these 2 species would show as much intraspecific variation as occurs in other species of the *Atropos* Group.

The truncate elevations on the left side of both *anisitsi* and *boliviensis* arise close to L2vm, extend dorsally, and their genitalia closely resemble those of *B. discoidalis*.

Undetermined species.— Several museum specimens were examined whose genitalia and phenotypic appearance did not fall into the known species. These were as follows:

1-2. *Blaberus* spp. *A* (Figs. 205, 213) and *B* (Figs. 206, 211, 212).— These 2 species from Peru, except for their much smaller size, resemble *colosseus*, particularly in their slender form and pale coloration. The preputial spines of both forms (cf. Figs. 211, 213) differ from each other. The anterior elevations of the left side are not much larger than those on the right, thus resembling the prepuce of *colosseus*.

3. *Blaberus* sp. *C* (Fig. 207).— This specimen from Colombia was identified by Hebard as *B. discoidalis*. However, it is considerably smaller and more slender than is *discoidalis*, and phenotypically resembles the specimen identified by Princis as *B. anisitsi* (Fig. 202). Its genitalia (Fig. 210) are unique (and differ from *anisitsi*, Fig.



Figs. 205-215. Males of *Blaberus* spp. The genitalia are from the adult males shown. 205, 213. *Blaberus* sp. A. (*Brasilianus* Group) (USNM), Tingo, Maria, Peru. 206, 211, 212. *Blaberus* sp. B. (*Brasilianus* Group) (USNM), Tingo, Maria, Peru. (Fig. 212 is an enlargement of the right and left sides of the prepuce shown in Fig. 211.) 207, 210. *Blaberus* sp. C. (*Atropos* Group) (USNM), Susumuco, Colombia. (The prepuce in Fig. 210 is broken and the spines on the lower left side normally lie under L2d.) (det. by Hebard as *B. discoidalis*). 208, 214. *Blaberus* sp. D. (*Brasilianus* Group) (ANSP), St. Laurent du Maroni, French Guiana (det. by Hebard as *B. giganteus*). 209, 215. *Blaberus* sp. E. (*Giganteus* Group) (USNM), Borba, Rio Madeira, Amazonas, Brazil. (Scale for adults = 10 mm; for genitalia = 0.3 mm.)

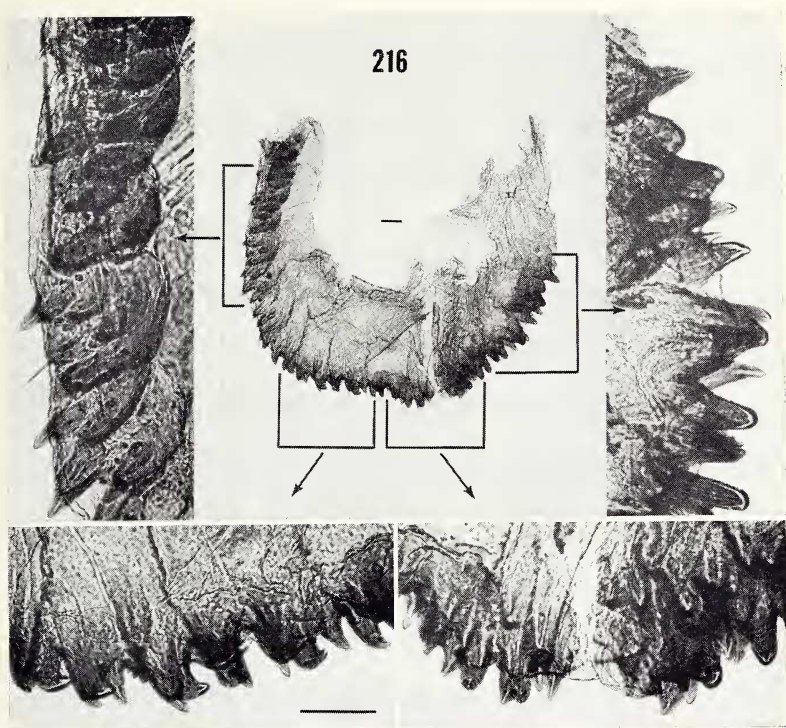
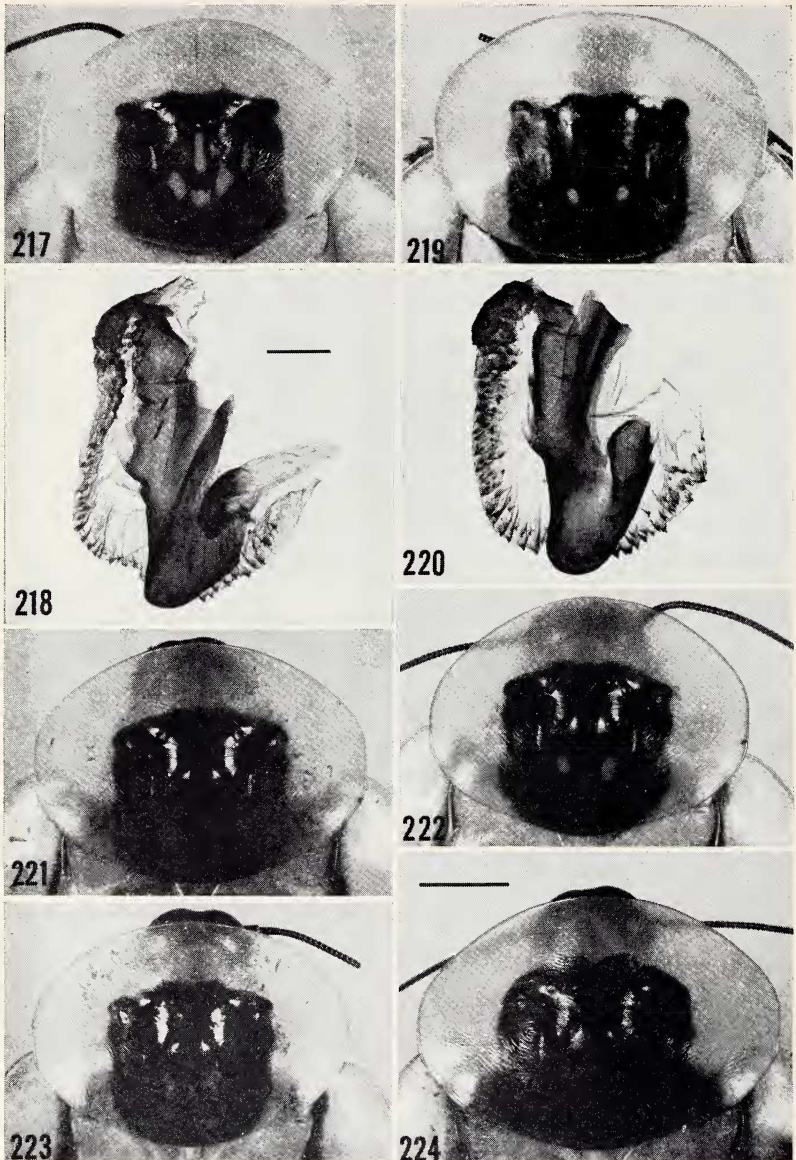


Fig. 216. Prepuce of *Blaberus* sp. (*Giganteus* Group). (MCZ), Andegoya, Colombia. Different portions (brackets) of the prepuce (center) are enlarged to show variations in the spines (scale = 0.1 mm).



Figs. 217-220. *Blaberus trapezoideus*. Pronotum and genitalia. 217-218. (BMNH). Paralectotype of *Blabera quadrifera* Walker. 219-220. (BMNH). Lectotype of *Blabera quadrifera* Walker. Oajaca, Vera Cruz, Mexico. 221-224. *Blaberus craniifer*. Variations in the shape of the pronotum in speci-

203) in that all of the spines bordering the prepuce are relatively large and arise from a well defined sclerotized margin; the shapes of the preputial spines also differ between these 2 specimens.

4. *Blaberus* sp. *D* (Fig. 208). — This is a species determined by Hebard as *B. giganteus* (from French Guiana) but its genitalia (Fig. 214) are that of a member of the *Brasilianus* Group. The truncate elevations on the left side of the prepuce are small and somewhat like those of *colosseus*, but the other spines are greatly reduced in size and number. This specimen is probably *colosseus* (though it is somewhat broader and more intensely colored than *colosseus* from Trinidad and Mexico, (cf. Figs. 112-115) in which the preputial spines have been greatly reduced (cf. Figs. 116-129).

5. *Blaberus* sp. *E* (Fig. 209). — This specimen is close to *giganteus* but is more slender and its general coloration is very pale. Its genitalia (Fig. 215) are massive and there are more rows of preputial spines than are usually found in *giganteus* (Figs. 28-40).

Distribution. — The species of *Blaberus* are almost entirely neotropical (Table 1). Four of the 5 species of the *Brasilianus* Group are restricted to South America; *colosseus* is more widely distributed and occurs in Mexico, Central and South America. Members of the *Giganteus* and *Atropos* Groups are found in Central and South America, and a few species occur in the West Indies, southern Florida, and Mexico.

Evolution of the aedeagus and prepuce. — I believe that the prepuce of *Giganteus* Group males which lack truncate elevations and have relatively simple, small preputial spines is the most primitive of the 3 groups of *Blaberus*. However, though the preputial spines are small they may vary in shape (Fig. 216) and some spines are reminiscent of those found in the *Brasilianus* and *Atropos* Groups. A *Giganteus* Grouplike form could have given rise to individuals of both the other 2 groups. The preputial spines of the *Brasilianus* Group are often numerous and may occur in multiple rows (e.g., Figs. 88, 90) like some individuals of the *Giganteus* Group (e.g., Figs. 36, 47, 215). In both the *Brasilianus* and *Atropos* Groups, the anterior elevations of the prepuce on the left side probably evolved from the left tumorlike outgrowth of a *Giganteus* Grouplike form. However, in the *Brasilianus* Group, the anterior elevations on the left and right sides do not differ greatly in size whereas there is a marked size difference between the elevations on the two sides in the

mens from a laboratory culture. (Scale for pronotum [see Fig. 224] = 5 mm.; scale for genitalia [see Fig. 218] = 0.5 mm).

Atropos Group. It is of interest that in occasional specimens of *B. discoidalis* (*Atropos* Group) the anterior elevations on the left side are so poorly developed (Fig. 184) that the lateral swelling of L2d resembles the outgrowth in the *Giganteus* Group.

In Princis' (1963) linear arrangement of 14 *Blaberus* spp., the species *minor* is separated from other members of the *Brasilianus* Group by *boliviensis* and *atropos*. I would rearrange this sequence and place *minor* with *brasilianus*, *fusiformis*, and *scutatus*.

Table 1. Geographical distribution of species of *B'aberus*.

Species	Distribution ^a
<i>Giganteus</i> Group	
<i>craniifer</i>	Mexico, Guatemala, British Honduras, Honduras, Costa Rica, Panama, Venezuela, Cuba, Dominican Republic, Florida (Key West)
<i>giganteus</i>	Mexico, Guatemala, Panama, Colombia, Venezuela, Trinidad, British Guiana, Surinam, French Guiana, Dominican Republic (?)
<i>Brasilianus</i> Group	
<i>brasilianus</i>	Brazil
<i>colosseus</i> ^c	Trinidad ^b , Mexico ^b , Guatemala, Costa Rica, Panama, Venezuela ^b , French Guiana
<i>fusiformis</i>	Brazil, Bolivia, Paraguay, Argentina
<i>minor</i>	Brazil, Bolivia, Paraguay, Argentina
<i>scutatus</i>	Brazil, Peru
<i>Atropos</i> Group	
<i>anisitsi</i>	Paraguay
<i>atropos</i>	Trinidad, British Guiana, Chile (?), Colombia ^b , Mexico ^b
<i>boliviensis</i>	Bolivia, Ecuador ^d
<i>discoidalis</i>	Costa Rica ^b , Dominican Republic ^b , Jamaica, Cuba, Haiti, Vieques Island, Panama, Colombia, Venezuela, Trinidad, Ecuador ^e , Nicaragua ^b , Florida (near Key West) ^f
<i>parabolicus</i>	Colombia, Surinam, Brazil, Peru, Ecuador, Bolivia

^aFrom Princis (1963) unless otherwise indicated; the localities for *craniifer* include those for *trapezoides*.

^bFrom present study.

^cLocalities from Hebard (1920).

^dFrom Princis (1952).

^ePrincis lists Ecuador with a ?. I have seen 1 specimen (Fig. 189) from Ecuador.

^fFrom A. B. Gurney (personal communication). (Record of USNM and Fla. Plant Board).

Chromosome numbers. — The diploid chromosome numbers of females of 5 species of *Blaberus* are: *giganteus*, 74; *craniifer*, 74; *atropos*, 74; *parabolicus*, 40; *discoidalis*, 38. The males have one less sex chromosome (Cohen and Roth, unpublished data). Evidently members of the *Atropos* Group have variable chromosome numbers.

Addendum: Since this paper went to press I have examined the lectotype and paralectotype of *Blabera quadrifera* Walker, which is a synonym of *B. trapezoideus* Burm. The pronotum of one of these specimens is illustrated by Princis (1958, p. 74). The tegmina of these 2 specimens are hairy, as they are in *B. craniifer*, and their genitalia (Figs. 218, 220) are indistinguishable from those of *craniifer* (cf. Figs. 47-57, 62-74). As for the laterally truncate pronotum of *trapezoideus* (Figs. 217, 219), the pronotal shape is so variable in light colored *craniifer* (Figs. 221-224) that this character cannot be used to distinguish the 2 species. I believe that *trapezoideus* (type locality Mexico) is the light colored form of *craniifer*. Both species were described by Burmeister (Handb. Ent. 2 (2), Berlin, 1838, p. 516). Because *B. craniifer* has been used widely as an experimental animal I select it as the valid name for this species.

SUMMARY

Based on the structure of the prepuce and aedeagus, species of *Blaberus* are placed in the following three groups: 1) *Giganteus* Group (*giganteus*, *craniifer*), 2) *Brasilianus* Group (*minor*, *brasilianus*, *colosseus*, *fusiformis*, *scutatus*), and 3) *Atropos* Group (*atropos*, *parabolicus*, *discoidalis*, *anisitsi*, and *boliviensis*).

I consider *Blaberus trapezoideus* to be a synonym of *B. craniifer*, and *B. colosseus*, formerly a synonym of *B. giganteus*, to be a valid species.

The genitalia are sufficiently distinctive to place individuals in their respective groups. However, intraspecific variation of the genitalia is so great that it is difficult and sometimes impossible to distinguish between certain species of a Group.

Three of the 5 species in the *Atropos* Group have variable chromosome numbers of 74, 40, and 38.

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